# THE GENERA OF SIMAROUBACEAE AND BURSERACEAE IN THE SOUTHEASTERN UNITED STATES ${ }^{1}$ 

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SIMAROUBACEAE A. P. de Candolle, Ann. Mus. Hist. Nat. Paris 17: 422. 1811, "Simarubeae."

(Quassia Family)
Trees and shrubs [rarely subshrubs], often with bitter bark. Leaves usually alternate, never glandular-punctate, pinnately compound or simple [rarely rudimentary], with predominantly entire margins, exstipulate [or stipulate]. Flowers usually small to minute, greenish or variously colored, hypogynous, regular, bisexual or unisexual by abortion, or both, with biseriate, [3]4-6[8]-, usually 5 -merous perianth, in terminal and/or axillary many- or few-flowered cymose panicles or racemes, rarely solitary. Sepals distinct or united, imbricate or valvate. Petals distinct, imbricate or valvate, rarely wanting. Stamens distinct, as many or twice as many as the petals [rarely more numerous], usually inserted at base of an intrastaminal disc, rudimentary or wanting in $i f$ flowers; filaments usually slender, sometimes appendaged at base on the ventral (adaxial) side; anthers usually versatile, 2- or rarely 4-locular at anthesis, introrse, longitudinally dehiscent. Intrastaminal nectariferous disc usually present, annular, cupular, cushion-like [to columnar], mostly lobed or crenate, rarely obscure or wanting. Gynoecium usually inserted on or encircled at base by the disc, sessile [or rarely raised on a gynophore], 2-6[8]-carpellate, apocarpous to syncarpous, rudimentary or wanting in ô flowers; stigmas distinct or united; styles basal, lateral or apical, distinct or partially to completely united; ovaries 1-carpellate and -locular (gynoecium apocarpous) or $2-3[4]$-carpellate and -locular with axile placentae (gynoecium syncarpous) ; ovules anatropous or rarely orthotropous to campylotropous, usually epitropous, very rarely apotropous, 2 - or rarely 1 -integumented, with a thick nucellus, 1 or 2 (collateral or superposed) [very rarely more

[^0]numerous] in a locule, pendulous from the top or ascendant from the base of the latter. Fruit apocarpous, of 2-6[8] one-carpellate and -locular drupes, [berries] or samaras, or a syncarpous, 2-3[4]-carpellate and -locular (occasionally 1 -locular by abortion) berry, samaroid capsule [drupe or schizocarp] with 1 -seeded locules. Seeds with membranaceous or leathery testa; endosperm scanty or wanting; embryo rather large, straight or rarely curved, with narrow, mostly fleshy, plano-convex or flat cotyledons and usually a very short radicle. (Including Surianaceae.) Type genus: Simarouba Aublet.

A pantropical family of about 30 genera and 200 species, at least two species in temperate eastern Asia. Four of twelve genera indigenous to the New World occur in subtropical Florida. One species of Ailanthus is also naturalized in our area.

The rather heterogeneous family includes six sharply delimited subfamilies. Evidence from wood anatomy supports the segregation of at least some as distinct families, but, since data from gross morphology appear to be inconclusive and those from floral anatomy, embryology, and cytogenetics of the family are fragmentary, it seems preferable to retain the family in the larger sense.

Simaroubaceae are closely related to Rutaceae and Burseraceae, differing from the former mainly in the absence of multicellular glands (secretory cavities) with aromatic oils in leaves, axes, and floral parts, and from the latter in the absence of schizogenous resin ducts in the bark.

Wood and/or bark of some species (e.g., Picrasma excelsa (Sw.) Planch., "Jamaica Quassia"; Quassia amara L., "Surinam Quassia") yield a bitter principle employed as tonics and vermifuges, as an insecticide, and sometimes as a substitute for hops in brewing. Some genera produce timber of local importance; a few species are ornamentals.

References:
Boas, B. Beiträge zur Anatomie und Systematik der Simarubaceen. Thesis, 58 pp. Dresden. 1912. [Also in Beih. Bot. Centralbl. 29(1): 303-356. 1913.]
Cronquist, A. Studies in Simaroubaceae-IV. Résumé of the American genera. Brittonia 5: 128-147. 1944. [Suriana, Recchia, Alvaradoa, Holacantha, Picrasma, Picrolemma, and Quassia are treated in detail.]
Desar, S. Cytology of Rutaceae and Simarubaceae. Cytologia 25: 28-35. 1960. [Ailanthus altissima, $2 n=80$, Quassia amara, $2 n=36$.]
Engler, A. Simarubaceae. Nat. Pflanzenfam. III. 4: 202-230. 1897; ibid. ed. 2. 19a: 359-405. 1931.

Hartl, D. Die Übereinstimmungen des Endokarps der Simarubaceen, Rutaceen, und Leguminosen. Beitr. Biol. Pfl. 34: 453-455. 1958.
Jadin, F. Contribution à l'étude des Simarubacées. Ann. Sci. Nat. Bot. VIII. 13: 201-304. pl. 1. 1901.
——. Essai de classification des Simarubacées basée sur les caractères anatomiques. Compt. Rend. Assoc. Fr. Avanc. Sci. 30(2): 477-483. 1902.* [See review in Bull. Soc. Bot. Fr. 49: 223, 224. 1902.]
Nair, N. C., \& T. S. Joseph. Floral morphology and embryology of Samadera indica. Bot. Gaz. 119: 104-115. 1957.
—_ \& R. K. Joshi. Floral morphology of some members of the Simaroubaceae. Bot. Gaz. 120: 88-99. 1958. [Five spp. of Ailanthus, including A. altissima; Picrasma quassioides (D. Don) Benn.. and Brucea sumatrana Roxb. (= B. amarissima (Lour.) Desv. ex Gomes).]
-_ \& N. P. Sukumaran. Floral morphology and embryology of Brucea amarissima. Bot. Gaz. 121: 175-185. 1960.
Narayana, L. L. Embryology of two Simaroubaceae. Curr. Sci. Bangalore 26: 323, 324. 1957.* [Includes Ailanthus excelsa.]

- \& M. Sayeeduddin. Floral anatomy of Simarubaceae - I. Jour. Indian Bot. Soc. 37: 517-522. 1958. [Quassia amara L. and Ailanthus excelsa.]
Record, S. J.. \& R. W. Hess. Timbers of the New World. 640 pp. pls. 1-59. New Haven. 1943. [Simaroubaceae, 509-514; Surianaceae, 521. 522.1
Sargent. C. S. Manual of the trees of North America (exclusive of Mexico). ed. 2. 897 pp . 1922. [Simaroubaceae. 641-645.]

Saunders. E. R. Floral morphology. Vol. 2. New York. 1940. [Simaroubaceae. 195-197.]
Small. J. K. Simaroubaceae. N. Am. Fl. 25: 22i-239. 1911. [Suriana placed in a separate family.]
Webber, I. E. Systematic anatomy of the woods of the Simarubaceae. Am. Jour. Bot. 23: 577-587. 1936.
West. E.. \& L. E. Arnold. The native trees of Florida. 212 pp. Gainesville. 1946. [Simaroubaceae, 101-104.]

Wiger. J. Embryological studies on the families Buxaceae. Meliaceae. Simarubaceae and Burseraceae. Thesis. Lund. 1935.* [See Mauritzon's criticism. Bot. Not. 1935: 490-502. 1935; Wiger's reply. Bot. Not. 1936: 585-589. 1936.]

## Key to the Gexera of Simarolbaceae

General characters: trees or shrubs with alternate predominantly pinnate leaves; flowers small. uni- or bisexual, or both; perianth double. usually 5-merous; stamens 5 or 10 , distinct; intrastaminal disc usually present; gynoecium apoor syncarpous. 2-5-carpellate; ovules 1 or 2 in each locule.
A. Leaves simple, small (not over 5 cm . long) and narrow: flowers bisexual. in short. terminal, few-flowered. corymb-like panicles. rarely solitary; stamens 10. the 5 antipetalous usually staminodial or rudimentary; intrastaminal disc wanting; carpels distinct; fruit of 5 or fewer achene-like drupelets; strand plant of subtropical Florida.

1. Striana.
A. Leaves pinnately compound; flowers usually unisexual (occasionally also bisexual) in large many-flowered, complex terminal panicles or racemes; intrastaminal dise distinct; carpels connate. sometimes only by the styles. rudimentary or wanting in $\delta$ flowers; fruits various, never achene-like drupelets.
B. Stamens 10 in $\delta$ flowers, much reduced or wanting in $ㅇ+$ flowers; carpels 4-6. usually 5 ; styles lateral. connate; ovaries distinct. connivent; fruits aggregate.
C. Leaves usually even-pinnate. persistent; leaflets alternate. $\pm$ leathery. entire; staminal filaments appendaged at base; fruit of 5 or fewer olive-shaped drupes about 2 cm . long; hammocks of subtropical Florida.
2. Simarouba.
C. Leaves odd-pinnate, deciduous; leaflets usually opposite, thin, with a few glanduliferous teeth or lobules near the base; staminal filaments without appendages; fruit of 5 or fewer oblong samaras $3-5 \mathrm{~cm}$. long, each with a flattened seed at the middle of the membranaceous wing; northern Florida and northward. ...............3. Ailanthus.
B. Stamens 5 and alternate with the sepals in of flowers, reduced or wanting in $P$ flowers; carpels 2 or 3 ; styles terminal, connate or distinct; ovary compound; leaves odd-pinnate; hammocks of subtropical Florida.
D. Leaflets $5-9,5-12 \mathrm{~cm}$. long; of and $\&$ flowers with linear-lanceolate petals, in terminal panicles with slender racemose or spikelike branches; stigma 2-lobed; style one, very short and stout; fruit a 1- or 2 -seeded berry.
3. Picramnia.
D. Leaflets 19-51, 1-3 cm. long; of flowers with linear-filamentous petals, the 9 flowers without petals, in terminal and axillary racemes; stigmas 3 ; styles 3 , distinct, subulate, short; fruit a flat, papery, 1 -seeded samaroid capsule.
4. Alvaradoa.

## Subfam. SURIANOIDEAE Engler

1. Suriana Linnaeus, Sp. Pl. 1: 284. 1753; Gen. Pl. ed. 5. 137. 1754.

Shrubs or small trees $1-8 \mathrm{~m}$. high with most parts more or less densely pubescent with simple and glandular hairs. Leaves sessile, simple, entire, narrow (seldom over 4 cm . long), thickish, with indistinct lateral veins and centric mesophyll. Flowers relatively small, bisexual, obdiplostemonous, with 2-bracteolate pedicels, in terminal, few-flowered, corymb-like cymose panicles (sometimes reduced to a solitary flower). Sepals 5, narrow (about 6-10 mm. long), connate at base, imbricate, persistent. Petals 5, yellow, broad, clawed, about as long as the sepals, imbricate. Stamens 10, distinct, the antipetalous usually antherless or rudimentary; filaments subulate, hairy below; anthers subcircular in outline, emarginate at both ends, introrse, 2-locular at anthesis; pollen grains medium sized, suboblate, 3-colpate, finely striate. Intrastaminal disc apparently wanting. Gynoecium apocarpous, 5 -carpellate; stigmas distinct, capitellate; styles distinct, filiform, nearly basal; ovaries 1-locular, sessile; ovules 2 (collateral), ascending from the base of the ovary locule, 1 -integumented, orthotropous, becoming campylotropous after fertilization. Fruits 1 -seeded achene-like drupelets (not over 5 mm . long) with thin flesh and crustaceous endocarp (stone), obovoid-subspherical, pubescent. Seeds broadly obovoid, slightly flattened laterally, endospermless, with a thin membranaceous testa; embryo horseshoe shaped, with flat, oblong cotyledons and an elongate radicle descendent toward the micropyle which is side by side and in contact with the hilum. Type species: S. maritima L. (Named in honor of Joseph Donat Surian, a French physician and botanist, "Dioscorides Americanus futurus" [Plumier, Nov. Pl. Am. Gen. 37. 1703], companion and collaborator of Plumier.) - Bay cedar.

A monotypic genus represented by Suriana maritima, widely but sporadically distributed on the seashores of the New and Old World tropics, but
apparently absent from the Pacific coasts of the Americas, the islands of the Central Pacific, and the Atlantic coast of Africa. It occurs in the coastal sand dunes and hammocks of the Florida Keys and of peninsular Florida northward to Brevard and Pinellas counties, and beyond our area in Bermuda, the West Indies, and from Yucatán south to Brazil. Millspaugh (Publ. Field Mus. Bot. 2: 241. 1907) believed the fruits (stones) to be carried on the feet of sea birds, but according to Guppy they "could readily be carried in the crevices of floating logs, or in the cavities of floating pumice, such as is stranded on the beaches of tropical regions all over the world. But it is on their great floating powers, which fit them for dispersal by currents, that we must mainly rely." Buoyancy of the stones is produced by the unfilled space in the fruit locule (Guppy, Schimper).

Record \& Hess (1943, p. 521), Small (Man. 761. 1933), Wilson (1911), and a few others thought the genus to represent a distinct, monotypic family Surianaceae; but, if a separate family is recognized, it should also include the closely related genera Cadellia F. Muell., Guilfoylia F. Muell., and perhaps also Recchia Sessé \& Moc. ex DC. (Rigiostachys Planch.).

The branches exude some kind of "manna."

## References:

See also under family references, Boas, Engler (1897, pp. 208, 209; 1931, pp. 367, 368), Jadin, Record \& Hess, Webber (pp. 577-579, 586, 587), and Wiger.
Guppy, H. B. Plants, seeds, and currents in the West Indies and Azores. 531 pp., 3 maps. London. 1917. [Fruit dispersal, 239-242.]
Rav, M. A. An embryological study of Suriana maritima Linn. Proc. Indian Acad. Sci. B. 11: 100-106. 1940.
Schimper, A. F. W. Die Indo-Malayische Strandflora. (Botanische Mittheilungen aus den Tropen. 3.) 204 pp., pls. 1-7. Jena. 1891. [Floating power of stones, 163, 165.]
Solereder, H. Ueber die systematische Stellung der Gattung Rigiostachys, zugleich ein Beitrag zur näheren Kenntnis der Simarubeae-Surianoideae. In: Loesener, T., \& H. Solereder. Ueber die bisher wenig bekannte südmexikanische Gattung Rigiostachys. Verh. Bot. Ver. Brandenburg 47: 41-61. 1905. [Includes morphology of ovules, fruits, and seeds.]

Wilson, P. Surianaceae. N. Am. Fl. 25: 225. 1911.

## Subfam. SIMAROUBOIDEAE

## Tribe Simaroubeae

## 2. Simarouba Aublet, Hist. Pl. Guiane Fr. 2: 859. 1775. ${ }^{2}$

Trees or large shrubs with bitter bark and wood. Leaves even-pinnate [or odd-pinnate], persistent; leaflets 3-21, mostly $8-16$, alternate, rarely opposite, entire, $\pm$ coriaceous, shortly petiolulate. Plants polygamo-dioecious or dioecious. Flowers small, unisexual or uni- and bisexual, obdiplo-

[^1]stemonous, in large terminal and axillary complex panicles. Sepals 4-6, usually 5, rather small, connate at least at base, imbricate. Petals 4-6, usually 5, yellowish to yellow [or whitish], much longer than the sepals, imbricate. Stamens $8-12$, usually 10 , as long as the petals, reduced, rudimentary or absent in $\&$ flowers; filaments subulate, broadened toward base, with an adaxial, liguliform, pubescent appendage at base; anthers oblong in outline, slightly emarginate, versatile, 2 -locular at anthesis; pollen grains small, subprolate, 3-colpate. Intrastaminal disc $\pm$ cushionlike, depressed in $\hat{\delta}$ flowers. Gynoecium (4)5(6)-carpellate, sessile on the disc, partially syncarpous, rudimentary or wanting in $\hat{\delta}$ flowers; stigmas 4-6, usually 5, long, slender, and divergent in of flowers, short, lobelike in bisexual flowers; styles connate into a short column; ovaries distinct, 1-locular, cohering [or perhaps sometimes weakly connate] by their ventral sutures and thus resembling a compound deeply lobed ovary; ovules solitary in each carpel, pendulous from near the top of the inner angle of the locule, anatropous and epitropous, 2 -integumented. Drupes 5 or fewer from each flower, ellipsoid to obovoid, slightly laterally compressed, usually 2 -ridged, with thin flesh and a crustaceous stone. Seeds endospermless; testa thin, membranaceous; embryo straight, with fleshy, plano-convex cotyledons and a very short, superior radicle partly included between the cotyledons (retracted). Type species: S. amara Aublet. (Name derived from the Carib Indian name of the type species in French Guiana.)

A tropical American genus of about six species. Simarouba glauca DC., paradise tree, occurs in coastal hammocks on the Florida Keys and in southern peninsular Florida (Dade, Broward, and Palm Beach counties). It is widely distributed in the West Indies and in Central America from Costa Rica to southern Mexico. The ellipsoidal fruits, about 2 cm . long, are scarlet, changing to dark purple or black when ripe. A white-fruited form has been reported from El Salvador.

The timber of some species, especially the South American Simarouba amara, is of commercial importance. The bitter bark of roots of S. amara and S. glauca is said to be efficient against diarrhea and post-dysenteric disorders. Seeds of S. glauca yield about 60 per cent of edible oil and a crystalline glycoside, glaucorubin, which reportedly has amoebicidal properties and is now being introduced in most of the major tropical areas under the trade name of "Glaumeba."

The genus is a representative of a very natural group, SimarouboideaeSimaroubeae, and is closely related to the tropical South American Simaba Aubl. and Quassia L. (monotypic, according to Cronquist), as well as to the tropical African Odyendea (Pierre) Engl.

## References:

See also under family references, Engler (1897, pp. 211, 213; 1931, pp. 372347), Record \& Hess (pp. 513, 514), Sargent (pp. 643, 644), Small (pp. 227229), and West \& Arnold (p. 102).

Armour, R. P. Investigations on Simarouba glauca DC. in El Salvador. Econ.

Bot. 13: 41-66. 1959. [Commercial importance and cultivation as a vegetable oil crop.]
Cronquist, A. Studies in the Simaroubaceae-II. The genus Simarouba. Bull. Torrey Bot. Club 71: 226-234. 1944.
Kryn, J. M. Simarouba, paradise-tree, marupa, Simarouba spp., family: Simaroubaceae. U. S. Forest Serv. Forest Prod. Lab. Rep. R. 1956. 10 pp. 1953.*
Kukachka, B. F. Marupa: Simarouba amara Aubl., Simaroubaceae. U. S. Forest Serv. Forest Prod. Lab. Rep. 1856. 4 pp. 1960.*
Sargent, C. S. Simaruba. Silva N. Am. 1: 89-92. pls. 38, 39. 1891.
Sola, F. de. Notes on the aceituno tree (Simaruba glauca DC.) and its adaptation as a vegetable oil crop. Ceiba 4: 351-358. 1956.

## Tribe Picrasmeae Engler

3. Ailanthus Desfontaines, Mém. Acad. Sci. Paris 1786: 265. 1788, nom. cons.

Trees, sometimes strong smelling. Leaves odd-pinnate, large, deciduous; leaflets opposite or alternate, thin, with a few glanduliferous, blunt teeth or lobules near base [or entire or rarely coarsely toothed to lobed throughout], petiolulate. Plants polygamo-dioecious. Flowers small, uni- and bisexual, obdiplostemonous, of unpleasant odor, pediceled, in large, terminal panicles. Sepals 5 (6), connate in the lower third or higher, imbricate. Petals 5 (6), longer than the sepals, greenish or yellowish, induplicatevalvate in aestivation. Stamens inserted at base of an intrastaminal disc, 10 (12) in of flowers, sometimes fewer in bisexual, much reduced and sterile or absent in $\circ$ flowers; filaments subulate, without appendages; anthers oblong or oblong-ovate in outline, versatile, 2-locular at anthesis, subintrorsely dehiscent; pollen grains small to medium sized, subspheroidal, 3-colpate, reticulate. Intrastaminal disc annular, thick, usually deeply $5(6)$ - or $10(12)$-lobed, or crenate, of receptacular origin. Gynoecium 5(6)-carpellate [rarely 3-carpellate], partially syncarpous [or apocarpous], sessile within the disc, rudimentary or absent in of flowers; stigmas distinct, tongue-shaped and divergent or $\pm$ capitellate; styles lateral, filiform, usually connate [or distinct]; ovaries 1 -carpellate and -locular, much compressed laterally, distinct but $\pm$ cohering by their sutures and resembling a compound, deeply lobed ovary; ovules anatropous, 2-integumented, solitary in each carpel, hanging from below the insertion point of the style. Fruit of (1)2-5 (6) distinct, oblong to oblong-elliptic samaras, each with a flattened seed at the middle of the thin, veiny, adaxially emarginate wing. Seeds lenticular, with thin, membranaceous testa and sparse, fleshy endosperm; embryo with flat, obovate to orbicular cotyledons and a short, superior radicle. Type species: A. glandulosa Desf. ( $=$ A. altissima (Mill.) Swingle). (Name derived from the Moluccan name for $A$. integrifolia Lam., ailanto, tree-of-heaven, in allusion to the height of the trees.) - Tree-of-heaven.

A primarily tropical genus of about 15 species, distributed in eastern
and southern Asia, the Philippines, Malaysia, Melanesia (east to the Solomon Islands), and northeastern Australia, extending into the Temperate Zone to northeastern China and Korea (to about $40^{\circ} \mathrm{N}$. Lat.). The northernmost species, Ailanthus altissima (Mill.) Swingle, Chinese tree-ofheaven, stinkweed, $2 n=80$, introduced into North America in 1784 as an ornamental tree, has become naturalized in native woodlands of the southeastern United States as far south as northern Florida. Northward and westward beyond our area it seems to be primarily a "weed" tree of cities, but the exact extent of naturalization needs to be more carefully recorded. An irregularly branched, rapidly growing tree which reproduces by seeds, stump sprouts, and root suckers, it becomes a weed difficult to eradicate. However, it has sometimes been used for fastening sterile, sliding declivities and for aforestation of bare hill and mountain slopes (Alps, Caucasus) and of grasslands (Asia Minor). The leaves contain a substance toxic to seedlings of many species of gymnosperms and angiosperms. "It is possible that the toxic substance is washed from the [fallen] leaves by the rain and influences the composition of plant communities" (Mergen).

Small flies and beetles have been recorded as pollinators in Ailanthus altissima, but bees must participate since it is regarded as an undesirable honey plant. Wind pollination is also possible (cf. Wodehouse). Floral anatomy has been studied in this and a few other species, embryology only in the Indian $A$. excelsa Roxb., $2 n=62$. Apparently only two chromosome counts have been recorded.

Wood of Ailanthus altissima and the other species appears to be of relatively little value, being used mostly for fuel, occasionally for cabinet work, musical instruments, etc. It also seems to be fit for paper pulp. Leaves and bark of A. altissima, and bark of a few other species are used locally in Asia as anthelmintics or antidysenterics.

The genus occupies a somewhat isolated position in the tribe Picrasmeae of Simarouboideae, representing a subtribe of its own.

## References:

The large number of references has been reduced here primarily to those either of general interest or dealing specifically with the southeastern United States. Under family references see Engler (1931, pp. 390-393), Desai (p. 39), Nair \& Joshi, Narayana, Narayana \& Sayeeduddin, and Small (p. 234). Anderson, E. The tree of heaven, Ailanthus altissima 1. A blessing and a curse. Missouri Bot. Gard. Bull. 49: 105-107. 1961.
Andreae, E. Uber abnorme Wurzelanschwellungen bei Ailanthus glandulosa. Thesis, 34 pp., 3 pls. Erlangen. 1894.
Campredon, J. Etudes des propriétés physiques et mécaniques de quelques bois exotiques. III. Le bois d'Ailante (Ailanthus glandulosa Desf.). Ann. Ec. Natl. Eaux Forêts Nancy 5: 211-217. 1934.*
Davies, P. A. Leaf arrangements in Ailanthus altissima. Am. Jour. Bot. 24: 401-407. 1937. [See also ibid. 26: 67-74. 1939.]
——. Floral glands in Ailanthus altissima. Trans. Ky. Acad. Sci. 11: 12-16. 1943.*
——. Leaf glands on Ailanthus altissima. Ibid. 12: 31-33. 1945.*
\& E. Bennett. Abnormal branching in Ailanthus. Jour. Hered. 20: 348, 349. 1929.
_ \& E. W. Theiss. Factors affecting the method of branching in Ailanthus altissima. Bull. Torrey Bot. Club 64: 229-233. 1937. [See also Davies, Bull. Torrey Bot. Club 63: 139-146. pl. 5. 1936.]
Illick, J. S., \& E. F. Brouse. The Ailanthus tree in Pennsylvania. Penn. Dep. Forests Waters Bull. 38. 29 pp. 1926. [Includes biology and prospects of the species.]
Kriz, V., M. Chlebek, \& M. Pekar. Ailanthus [altissima] from the viewpoint of breeding. (In Czech.) Lesn. Práce 36: 116-118. 1957.*
Merendr, A. Ailanthus: cellulose plant. (In Italian.) Gior. Agr. Roma 66: 137. 1956.* [See also A. del Lungo, Terra Sole 122: 345-349. 1952.*]

Mergen, F. A toxic principle in the leaves of Ailanthus. Bot. Gaz. 121: 32-36. 1959. [A. altissima.]

Müller, R. Zur Anatomie der Ailanthus-Rinden. Pharm. Praxis 7: 261-263. 1908.* [For review see Bot. Jahresb. 36(1): 473, 474. 1908.]

Petaj, V. Die extrafloralen Nektarien auf den Blättern von Ailanthus glandulosa. (In Croatian.) Rad Jugosl. Akad. Znan. Umjet. 215: 59-81. 1916.* [For review see Bot. Centralbl. 137: 385. 1918.]
Saya, I. Ferite su fusto di Ailanthus glandulosa Desf. e reazioni di gemme dormienti. Nuovo Gior. Bot. Ital. II. 64: 680-682. 1957. [Wounds on the stem of $A$. altissima and reactions of dormant buds.]
Swingle, W. T. The early European history and the botanical name of the tree of heaven, Ailanthus altissima. Jour. Wash. Acad. Sci. 6: 490-498. 1916.

Tieghem, P. van. Ailante et Pongèle. Ann. Sci. Nat. Bot. IX. 4: 272-280. 1906. [Segregation of Pongelion Adans. from Ailanthus.]

Wodehouse, R. P. Hayfever plants. xx +245 pp. Chronica Botanica. Waltham, Mass. 1945. [Ailanthus altissima, 115, 116.]

## Subfam. PICRAMNIOIDEAE Engler

4. Picramnia Swartz, Prodr. Veg. Ind. Occ. 2, 27. 1788, nom. cons.

Trees or shrubs, usually with slender, curving branches, the bark and wood often very bitter. Leaves odd-pinnate, persistent; leaflets [3]5-9[21], opposite or alternate, entire, chartaceous to $\pm$ coriaceous, petioluled. Plants dioecious [or occasionally polygamous]. Flowers minute, unisexual [occasionally also bisexual]. Inflorescences paniculate, terminal [sometimes opposite the leaves], with slender, raceme- or spikelike branches. Sepals 5 [3 or 4], connate from $1 / 4$ to $1 / 2$ of their length, imbricate. Petals 5 [3 or 4, or wanting], narrowly linear-lanceolate [or lanceolate], as long [or twice as long] as the sepals, imbricate. Stamens as many as and opposite the petals, inserted below and between the lobes of a low intrastaminal disc, reduced to staminodia in $\$$ flowers; filaments subulate; anthers basifixed, almost globular, with thick connective, introrse, 4-locular at anthesis. Gynoecium 2 (3)-carpellate, syncarpous, rudimentary in of flowers; stigma deeply 2 -lobed, the lobes thick, divergent; style very short and stout, usually inconspicuous; ovary sessile, 2 (3)-locular; ovules anatropous, epitropous, 2 -integumented, pendulous from near the top of the carpels, 2 in
each locule. Fruit a rather juicy, subglobular, ellipsoidal or obovoid berry, (3) 2- or (by abortion) 1-locular, with 1 -seeded locules. Seed ovoid, often plano-convex, filling the cavity of the locule, the testa membranaceous, adnate to the undifferentiated embryo; endosperm wanting. (Pseudobrasilium Adans., 1763 ; Tariri Aubl., 1775 ; nom. rejic.) Type species: P. antidesma Swartz. (Name derived from Greek, pikros, bitter, and thamnos, shrub, in allusion to the bitterness of the vegetative parts.) - Bitterbush.

A genus of about 40 species of tropical American distribution. Picramnia pentandra Sw., a shrub or small, slender tree, of the West Indies, Colombia, and Venezuela, occurs in our area in the coastal hammocks of southeastern peninsular Florida (Dade County) and on the Florida Keys. Berries of this species are olive-shaped, $9-15 \mathrm{~mm}$. long, red, turning black when fully ripe; the seeds are light brown and lustrous. Leaves, bark, and roots of this and other species have been used locally in the tropics as febrifuges.

The genus, which represents a subfamily of its own, is in need of a revision.

## References:

Under the family references see Engler (1931, pp. 402, 403), Record \& Hess, Sargent, Small, and West \& Arnold (p. 101).
Radlkofer, L. Ueber die Gliederung der Familie der Sapindaceen. Sitz-ber. Akad. Wiss. München II. 20: 105-370. 1890. [Picramnia, relationship with Alvaradoa, 139-143.]

## Subfam. ALVARADOIDEAE Engler

5. Alvaradoa Liebmann, Vid. Medd. Nat. For. Kjøbenh. 1853: 100. 1854.

Shrubs or trees up to 15 m . high, with slender, terete, pubescent [or glabrous] branchlets and bitter bark. Leaves odd-pinnate, many-foliolate, crowded at the end of branches, apparently persistent; leaflets alternate, small (not over 5 cm . long), thin and firm [or leathery], entire, petiolulate. Plants dioecious. Flowers minute, unisexual, in slender, manyflowered, axillary or terminal racemes. Sepals 5, usually distinct in $q$ flowers and variously connate from near the base to the half of their length in of flowers, valvate. Petals 5, linear-filamentous, present [or absent] in $\delta$ flowers, wanting in $\&$ flowers. Stamens 5, alternate with the sepals, inserted below and between the lobes of the disc, wanting in $ㅇ$ flowers; filaments filiform, hairy in the lower part; anthers basifixed, oblong in outline, with a conspicuous, almost orbicular, swollen connective and introrse anther-halves, 4-locular at anthesis; pollen grains small, prolate-subspherical, 3-colpate. Intrastaminal disc thickish, deeply 5-lobed in $\hat{\text { o }}$ flowers, thin and scarcely lobed in ㅇ flowers. Gynoecium 3-carpellate (but only 1 carpel fertile), syncarpous, sessile on the disc, wanting in $\hat{o}$ flowers; stigmas small, simple; styles 3, distinct, subulate, short, recurved; ovary densely villous, flattened, obtusely triangular in cross sec-
tion, imperfectly 2 - or 3-locular on account of 2 incomplete partitions (apparently deeply intruded parietal placentae) demarcating a sole fertile locule in the obtuse angle of the ovary; ovules 2 in the fertile locule, basal, ascendent, anatropous, apotropous, 2 -integumented. Fruit a compressed, $2[3]$-winged, $\pm$ papery samaroid capsule [or leathery samara], crowned by remnants of the styles, appearing 3- or 1-locular, with 1 seed in the lower half. Seeds $\pm$ terete, narrowly ellipsoidal (the shape of rice grains) [or rather compressed and broadly elliptical in outline]; testa membranaceous; endosperm wanting; embryo straight, with plano-convex [or flat], fleshy cotyledons and a short, inferior radicle. Type species: A. amorphoides Liebm. (Named in commemoration of Pedro de Alvarado, one of the chief aides of Hernando Cortez in the conquest of Mexico.)

A genus of about five species, the range disjunct, including southern Florida, the West Indies, Mexico, and Central America, Bolivia, and Argentina. Alvaradoa amorphoides occurs in a few hammocks in southern peninsular Florida (Dade County) and the Florida Keys and in the West Indies, Mexico, and Central America.

Although the genus was originally placed with the Sapindaceae, Radlkofer showed Alvaradoa to be simaroubaceous with the closest relationship to Picramnia. Engler, however, placed the two in separate unigeneric subfamilies.

## References:

See also under family references, Cronquist (pp. 132-137), Engler (1931, p. 404), Record \& Hess (p. 510), Sargent (pp. 644, 645), Small, and West \& Arnold (p. 104).
Radlkofer, L. Ueber die Gliederung der Familie der Sapindaceen. Sitz-ber. Akad. Wiss. München II. 20: 105-370. 1890. [Alvaradoa, morphology of the flowers and fruits, relationship with Picramnia, 139-143.]

## BURSERACEAE Kunth, Ann. Sci. Nat. 2: 346. 1824. <br> (Torchwood Family)

Trees or shrubs, the inner bark with resin ducts. Leaves alternate, usually once pinnate, deciduous [or persistent], usually exstipulate. Flowers small, hypogynous, regular, apopetalous, usually unisexual by abortion, 3 - 5 -merous, in axillary [or terminal] cymose panicles. Plants mostly dioecious. Stamens 6-10, usually distinct, inserted below an intrastaminal [rarely extrastaminal] nectariferous disc; anthers versatile, introrse, longitudinally dehiscent, sterile in of flowers. Gynoecium 3[2-5]carpellate, .syncarpous, rudimentary or wanting in $\hat{\alpha}$ flowers; ovary $3[2-5]$-locular, with axile placentae; ovules anatropous, epitropous, 2 in each locule. Fruit usually drupaceous, with $\pm$ dry [or fleshy] exo- and mesocarp, dehiscent by valves [or indehiscent]; stones solitary [or 2-5], $3[-5]$-, usually 1 -locular by reduction or abortion of 2 locules. Seeds without endosperm, solitary in each locule; embryo straight [or curved],
cotyledons contortuplicate [or flat], usually $\pm$ deeply lobed, radicle superior. Type genus: Bursera Jacq. ex L.

A pantropical family of 15 or 16 genera and about 600 species. Six genera (including Bursera and Protium) with about 200 species occur in the New World. The family is subdivided into the tribes Protieae Engl., Bursereae [H. J. Lam] (Boswellieae Engl.), and Canarieae Engl. The subdivisions, although based exclusively upon the structure of the fruits, seem to be rather natural ones.

Burseraceae are closely allied with Rutaceae, Simaroubaceae, and Meliaceae. A close relationship to Anacardiaceae, proposed by some taxonomists (e.g., Radlkofer), is supported by evidence from anatomy and palynology.

Resinous substances obtained from some species are of economic significance. The most important of these are myrrh, from Commiphora molmol Engl. and C. abyssinica (Berg) Engl., and olibanum or frankincense, from species of Boswellia, especially B. Carteri Birdw. Myrrh is used in perfumery, and both are used in medicine and as incense.

## References:

See also Radlkofer under Alvaradoa (Simaroubaceae).
Engler, A. Burseraceae et Anacardiaceae. In: Candolle, A. \& C. de. Monogr. Phaner. 4: 1-573. pls. 1-15. 1883. [Burseraceae, 1-169. pls. 1-3.]
-_. Burseraceae. Nat. Pflanzenfam. ed. 2. 19a: 405-456. 1931.
Guillaumin, A. Répartition géographique et biologie des Burséracées. Revue Gén. Bot. 20: 321-327. pls. 11-14. 1908.
——. Les produits utiles des Burséracées. 73 pp. Paris. 1910.
. Recherches sur la structure et le développement des Burséracées. Ann. Sci. Nat. Bot. IX. 10: 1-302. 1909.
Heimsch, C., Jr. Comparative anatomy of the secondary xylem in the "Gruinales" and "Terebinthales", of Wettstein with reference to taxonomic grouping. Lilloa 8: 83-198. pls. 1-17. 1942. [Burseraceae, 122-124.]
Jadin, F. Recherches sur la structure et les affinités des Térébinthacées. Ann. Sci. Nat. Bot. VII. 19: 1-51. 1894. [Terebinthaceae divided into tribes Anacardieae and Bursereae.]
Lam, H. J. Beiträge zur Morphologie der Burseraceae insbesondere der Canarieae. Ann. Jard. Bot. Buitenzorg 42: 97-226. pls. 9-16. 1932. |Pinnate leaves of Burseraceae and related families are considered phylogenetically reduced shoots; but cf. Sinia, 1938.]
——. The Burseraceae of the Malay Archipelago and peninsula, with annotations concerning extra-Malayan species, especially of Dacryodes, Santiria, and Canarium. Bull. Jard., Bot. Buitenzorg III. 12: 281-561. 1932. [The "General Part," 281-317, contains many important data on morphology, dispersal, and phylogeny of the family.]
Leenhouts, P. W., C. Kalkman, \& H. J. Lam. Burseraceae. In: C. G. G. J. van Steenis, Fl. Males. I. 5: 209-296. 1955. [Includes notes of general interest on ecology, dispersal, distribution, wood anatomy, morphology, and taxonomy.]

Marchand, L. Recherches sur l'organisation des Burséracées. 56 pp., pls. 1-6. Paris. 1868.
Narayana, L. L. Microsporogenesis and female gametophyte in Boswellia serrata Roxb. Curr. Sci. Bangalore 28: 77, 78. 1958.*
——. Studies in Burseraceae. I. Jour. Indian Bot. Soc. 39: 204-209. 1960. [Boswellia serrata and Garuga pinnata Roxb., floral anatomy.]
——. Studies in Burseraceae. II. Ibid. 402-409. 1960. [Bursera serrata Colebr. ( $=$ Protium serratum (Wall. ex Colebr.) Engl.), floral anatomy and embryology; Garuga pinnata, embryology.]
Record, S. J., \& R. W. Hess. Timbers of the New World. 640 pp., pls. 1-59. New Haven. 1943. [Burseraceae, 105-110.]
Rose, J. N. Burseraceae. N. Am. Fl. 25: 241-261. 1911.
Sargent, C. S. Manual of the trees of North America (exclusive of Mexico). ed. 2. 897 pp. 1922. [Burseraceae, 645-648.]
Shukla, R. D. Studies in the family Burseraceae - I. Floral anatomy of Balsamodendron mukul Hook. Agra Univ. Jour. Res. Sci. 4: 567-573. 1955.*
——. Gametophyte in Balsamodendron mukul. Curr. Sci. Bangalore 23: 333. 1954.*

Sinia, H. R. Zur Phylogenie der Fiederblätter der Burseraceen und verwandter Familien. Ann. Jard. Bot. Buitenzorg 48: 69-100. pls. 13, 14. 1938. [Against Lam's theory of the caulomic nature of pinnate leaves of Burseraceae and their allies.]
Webber, I. E. Systematic anatomy of the woods of the "Burseraceae." Lilloa 6: 441-465. pls. 1-4. 1941.
Wiger, J. Embryological studies on the families Buxaceae, Meliaceae, Simarubaceae and Burseraceae. Thesis. Lund. 1935.*

1. Bursera Jacquin ex Linnaeus, Sp. Pl. ed. 2. 1: 471. 1762; Gen. Pl. ed. 6. 440. 1764, nom. cons.
Trees [or shrubs]. Leaves odd-pinnate [sometimes bipinnate], 3-9[-many]-foliolate [rarely 1 -foliolate], usually crowded at the end of branchlets, deciduous; leaflets opposite, chartaceous to subcoriaceous [or coriaceous], entire [or toothed], manifestly petiolulate [to sessile]. Flowers very small, unisexual [and/or bisexual], in axillary, raceme-like panicles, appearing prior to or with [or after] the leaves. Plants dioecious [or polygamous? ]. Sepals $3-5$, minute, connate at least at base, imbricate in bud. Petals $3-5$, whitish to creamy, much longer than the sepals, spreading and recurved, induplicate-valvate in bud. Stamens 6-10, nonfunctional in $\&$ flowers; filaments subulate; anthers oblong in outline, dorsifixed near the base, shorter and without pollen in $\&$ flowers; pollen grains medium-sized, 3-colpate, reticulate-striate. Intrastaminal disc annular, 6-10-lobed, orange or red. Stigma capitate, 3-lobed; style short, ovary sessile, ovoid, 3 -carpellate and -locular, with 2 collateral, pendulous ovules in each locule, rudimentary in ô flowers. Drupes subglobular or obliquely ellipsoid, indistinctly triangular, with resinous, fleshy, leathery exo- and mesocarp detaching in 3 [or 2] valves when the fruit matures; stones (bony endocarp) covered with a thin, membranaceous, light-pink coat (probably the innermost layer of mesocarp remaining attached to the
endocarp), usually solitary, attached to the persistent axis of the ovary, ovoid-trihedral, essentially 1 -locular, but bearing 2 minute, sterile locules or rudimentary stones in the upper half on the adaxial (ventral) side, usually 1 -seeded. Seeds without endosperm; testa membranaceous; embryo straight [or curved] with foliaceous, contortuplicate cotyledons and a short superior radicle. Germination epigeous, cotyledons 3 -fid, the first leaf 3 -foliolate. (Elaphrium Jacq., 1760; Simaruba Boehmer, 1760; nom. rejic.) Type species: B. gummifera L. ( $=$ B. Simaruba (L.) Sarg.). (Named in honor of Joachim Burser, 1583-1639, a German physician and botanist.)

A genus of about 100 species of tropical America. Bursera Simaruba (Elaphrium Simaruba (L.) Rose), gumbo-limbo or West Indian birch, of the West Indies, Mexico, Central America, and northern South America, occurs in coastal hammocks on the Florida Keys and in peninsular Florida about as far north as Brevard and Pinellas counties. Easily recognizable by its lustrous, smooth, copper-colored bark which exfoliates in thin, papery layers as in some species of Betula, in winter the tree (to 20 m .) is conspicuously leafless, in contrast with its evergreen associates. The species is a common "fence-post" tree in tropical America, for pieces of the trunk or branches set in the ground quickly develop roots and grow into trees. The Mexican B. fagaroides (HBK.) Engl. and B. microphylla Gray occur in southern Arizona, the latter in southeastern California as well.

Insect pollination has been presumed for the genus, but no data are available. Bursera Simaruba apparently is dioecious; records of polygamy are in need of verification. Staminate flowers in this species are 5 -merous (or more rarely 4 -merous). while the carpellate appear to be almost invariably 3 -merous and only very rarely 4 -merous.

The species of Bursera yield a fragrant glutinous resin which is locally applied in domestic medicine. The resin of $B$. Simaruba is also used as a substitute for glue and as cement for mending broken china and glass.

The genus seems to be most closely related to the paleotropic Boswellia Roxb. ex Colebr.

## Referexces:

See also under family references. Exgler (1931, pp. 423-429). Record \& Hess. Rose, and Sargent.
Bullock. A. A. Contributions to the flora of tropical America: XXVII. Notes on the Mexican species of the genus Bursera. Kew Bull. 1936: 346-387. 1936. [Includes key: economic notes, and references to economic uses and anatomy. See also Kew Bull. 1937: 447-457. 1937. and 1938: 163-168. 1938. for further notes, including the identification of Hinton's Mexican collections.]
Sargent. C. S. Bursera. Silva N. Am. 1: 95-98. pls. 41, 42. 1891.
West. E.. \& L. E. Arvold. The native trees of Florida, 212 pp . Gainesville. 1946. [B. Simaruba, 105.]


[^0]:    ${ }^{1}$ Prepared for a generic flora of the southeastern United States, a joint project of the Arnold Arboretum and the Gray Herbarium of Harvard University which has been made possible through the support of George R. Cooley and the National Science Foundation. This treatment follows the pattern established in the first paper in the series (Jour. Arnold Arb. 39: 296-346. 1958) and continued through the seventeen subsequent papers in volumes 40-43 (1959-1962). It should be repeated that the area covered by this work is bounded by and includes North Carolina, Tennessee, Arkansas, and Louisiana. The descriptions are based primarily on the plants of this area, with any supplementary material in brackets. References which the author has not seen are marked by an asterisk.
    The author is indebted to Dr. Carroll E. Wood, Jr., for his criticism and valuable suggestions, and to Mrs. Gordon W. Dillon, for her careful help in the preparation of the manuscript.

[^1]:    ${ }^{2}$ Aublet's generic name should be conserved against its earlier homonym, Simaruba Boehmer, 1760 [nom. rejic. vs. Bursera Jacquin ex Linnaeus, 1762, nom. cons.]. See A. A. Bullock, Taxon 8: 199. 1959.

